

THE SUBFAMILIES OF FORMICIDÆ, AND OTHER
TAXONOMIC NOTES.¹

BY WILLIAM MORTON WHEELER.

A comparison of the seventh volume of Dalla Torre's "Catalogus Hymenopterorum," which summarizes what was known of the classification of the Formicidæ down to 1890, with any very recent monograph of these insects, gives the impression that there has been no change in expert opinion concerning the limits of the family and its subfamilies during the past thirty years. Dalla Torre recognizes five subfamilies, the Dorylinæ, Ponerinæ, Myrmiciniæ, Dolichoderinæ and Camponotiniæ and the same groups are retained in Emery's contributions to the "Genera Insectorum" (1910-'13), so far as published, and in his recent sketch of the classification of the Myrmiciniæ (1914). Between the appearance of the "Catalogus" and the works just mentioned, however, Emery, who has shown greater interest than other myrmecologists in the definition of taxonomic categories above the rank of the genus, proposed an additional subfamily, the Pseudomyrminæ in 1899, and in 1895 transferred a group of genera, comprising the tribe Cerapachyini, from the Ponerinæ, where it had been placed by Forel in 1893, to the Dorylinæ. After Forel and I had objected to this proceeding, Emery, in the "Genera Insectorum" (1913) returned the Cerapachyini to the Ponerinæ, but gave them the rank of a section, the Prodorylinæ. He had long since reunited the Pseudomyrminæ with the Myrmiciniæ. In his most recent sketch of the classification of this subfamily (1914) he unites the tribes Metaponini and Pseudomyrmini as the first section, the Promyrminæ, and places all the other tribes in a second section, the Eumyrmiciniæ. Thus in 1920 the five subfamilies have again acquired the limits which they had in 1890.

During the past year a study of ant-larvæ, representing more than a hundred genera and many subgenera of all five subfamilies, has convinced me that Emery was right in 1899, when he regarded the Pseudomyrminæ as constituting an independent subfamily. I am also of the opinion that the Cerapachyini should be removed

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from the Ponerinae and raised to the rank of an independent subfamily, between the Dorylinae and Ponerinae. A number of reasons may be adduced for making these changes.

In 1899 Emery, after a comparative study of the larvæ of several Formicid genera, concluded that "Those of *Sima* and *Pseudomyrma*, besides their extremely hypocephalic development, exhibit a very special character in the presence of rudiments of antennæ. I believe that this very noteworthy fact, together with the well-known peculiar characters of the head of the imagines, will justify the separation of these genera from the remainder of the Myrmicinae, to form the new subfamily of the Pseudomyrminæ." My study of numerous species of this group, which now embraces four genera, *Tetraponera* Smith (= *Sima* Roger), *Pachysima* Emery and *Viticicola* Wheeler of the Old and *Pseudomyrma* Lund of the New World, shows that Emery was far from realizing the full import of their larval characters. Not only have the larvæ peculiar long, straight, cylindrical, distinctly segmented bodies with blunt anterior and posterior ends, a large, usually subquadrate head, ventrally placed and with rudiments of antennæ (which are also present in the larvæ of many other ants, notably in the Ponerinae), but the thoracic and first abdominal segments are furnished with peculiar exudatory papillæ (exudatoria), which form a cluster around the mouth. I have described and figured these organs in *Viticicola* and *Pachysima* (1918b) and have shown that they have the form of extraordinary appendages in the first larval stage (trophidium) of the two known species of the latter genus, and that the swollen ventral portion of the first abdominal segment, just behind the mouth, forms a pocket in which the workers place a pellet of food. The exudatoria, the pocket, which I call the *trophothylax*, and the unusual method of feeding are characteristic of all four genera and no distinct traces of such conditions have been found in any other ant-larvæ.

More recent study has added two very interesting facts, which, in advance of a complete account to be published in collaboration with my colleague, Prof. I. W. Bailey, may be briefly considered in this place. The food pellet proves to be merely the small pellet ("corpuscule enroulé," or "corpuscule de nettoyage" of Janet) which the worker ant moulds in its own infrabuccal pocket and consists of the solid food-particles from which the juices are

sucked, *plus* the various particles collected by the ant by means of the strigils of the fore tibiæ from the surfaces of the antennæ and other parts of the body and carried into the infrabuccal pocket after being wiped off by the maxillæ. Other ants eventually spit out the pellet which is commonly a moulded, subspherical conglomerate of diverse particles, such as small pieces of insects, fragments of plant tissue, fungus spores and hyphæ, pollen grains, etc., and cast it away as refuse, but the worker nurses of the *Pseudomyrmicæ* place it as pabulum in the trophothylax of the larva!

Even this, however, is not the whole story. An examination of the mouth of the larva reveals a singular structure, evidently used for reducing the food pellet to such a finely divided state that it can, when acted on by the digestive juices of the mesenteron, yield a certain amount of nutriment, which the worker ant could not extract from it while it was in the infrabuccal pocket. This larval structure, which may be called the *trophorhinium*, consists of two flat, opposable plates, the dorsal and ventral surfaces of the buccal cavity, each furnished with very fine, parallel, transverse striæ or welts, which, under a high magnification are seen to be made up of minute chitinous projections or spinules. The ventral usually has more numerous rows of spinules than the dorsal surface. The two surfaces are evidently rubbed on one another and thus triturate the substance of the food pellet, only small portions of which are ingested at a time from the trophothylax. In all *Pseudomyrmicæ* larvæ and in many larvæ of the other subfamilies, except the *Dorylinæ* and *Cerapachyinaæ*, the trophorhinium is beautifully developed, although in many ants (*Ponerinaæ*) it may be used for comminuting parts of insects given directly to the larvæ by the workers. A detailed description of the organ and of its extraordinary variations of structure in the various genera of *Formicidæ* is reserved for future publication.

In its development the trophorhinium bears a strange resemblance to the stridulatory organs of the petiole and postpetiole of many adult *Ponerinaæ* and *Myrmicinaæ*. It may, in fact, function also as a stridulatory organ, when the food supply is exhausted, and thus apprise the worker nurses of the larva's hunger. Many ant-larvæ, notably those of the *Ectatommiine Ponerinaæ* and of most genera of *Camponotinaæ* (*Formicinaæ*), also have elaborate but coarser stridulatory surfaces on the mandibles, so that the larva

may be able to produce a variety of sounds and therefore apprise the nurses of more than one need or craving.

The adult *Pseudomyrmicæ* are so peculiar in structure that Emery, Ashmead (1905) and others have been led to separate them sharply from all other *Myrmicinæ*. The shape of the head in the worker and female and especially of the clypeus and frontal carinæ is unique, the eyes are very large and there is a strong tendency to development of ocelli in the workers, the conformation of the petiole, postpetiole and tibial spurs is peculiar, and as I have recently shown (1919b), the number of antennal joints (12) is the same in the male as in the worker and female in all four genera.

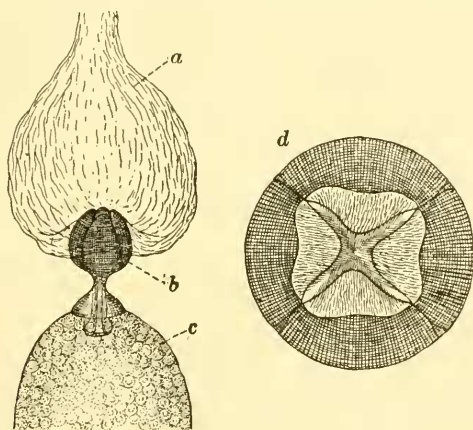


Fig. 1. *a*, Ingluvies, or "crop," *b*, calyx of proventriculus, or "gizzard," and *c*, ventriculus, or "stomach," of *Pachysima aethiops* Fabr.; *d*, proventriculus seen from the front under a higher magnification.

Little study has been devoted to the structure of the proventriculus, or "gizzard" in the *Myrmicinæ*, but Meinert, Forel and Emery have described and figured it as simple and tubular in most genera and of a very primitive type compared with the conditions in the *Dolichoderinæ* and *Camponotinæ*. I find, however, that the proventriculus of all four genera of the *Pseudomyrmicæ* is much more specialized, being anteriorly developed as an apple- or quince-shaped ball, covered with longitudinal and circular muscles and with four distinct, connate sepals, bluntly rounded and finely hairy at their tips, and posteriorly as a very short, tubular, con-

stricted portion which projects as a button into the cavity of the ventriculus (Figs. 1 and 2). The peculiarities mentioned seem to me to justify us in returning to Emery's contention of 1899 that the Pseudomyrmicæ constitute an independent subfamily. I have endeavored to show in a recent paper (1919a) that neither the larval nor the imaginal Metaponini can be regarded as at all closely related to the Pseudomyrmicæ. Emery's section Promyrmicini should therefore be abandoned and his term Eumyrmicini may be regarded as merely synonymous with Myrmicini.

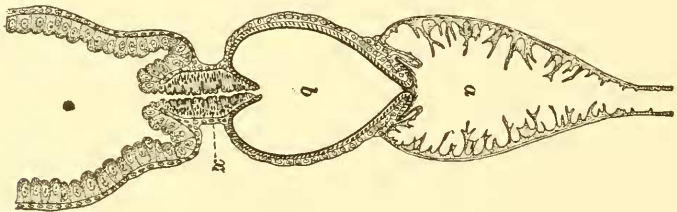


Fig. 2. *Viticicola tessmanni* Stitz; *a*, sagittal section through part of the alimentary tract, including *a*, the ingluvies, or "crop" (much contracted); *b*, calyx of proventriculus, or "gizzard," *x*, its cylindrical portion, and *c*, anterior portion of ventriculus, or "stomach."

A study of the larvæ of the Cerapachyini shows that they are extremely like the larvæ of the Dorylinæ. This was noticed by Emery in his observations on the larva of *Acanthostichus serratulus* (1899). The mandibles are small, narrow, pointed and rather feebly chitinized, and I have failed to find a trophorhinium in either group. Apparently the young are fed only on soft food. That the foraging habits of certain Cerapachyini (*Phyracaces*) resemble those of the Dorylinæ was shown in my paper on the Australian species (1918a). We know nothing of the pupæ, but they are probably not enclosed in cocoons as in the Ponerinæ. Although the worker of the Cerapachyini has a Ponerine habitus, the characters of the female in the various genera are peculiarly diverse. In some cases (*Phyracaces*), this caste is winged and not unlike the females of certain Ponerinæ, in others (*Parasyscia*, *Eusphinctus*) the female is wingless and ergatomorphic and in still others (*Acanthostichus*, *Nothosphinctus*) the female is so much like the corresponding caste in the Dorylinæ, that it might be regarded

as a dichthadiigyne. A similar diversity is seen in the males of the Cerapachyini. The male of *Acanthostichus afflictus*, recently discovered by Gallardo (1919) in Argentina, is so much like an *Eciton* or *Dorylus* male that even an expert myrmecologist would not hesitate to place it among the Dorylinae. The males of other genera (*Lioponera*, *Phyracaces*, *Cerapachys*, *Eusphinctus*) on the other hand, though lacking the cerci, have a decidedly Ponerine habitus. It would seem, therefore, that the Cerapachyini are intermediate between the Dorylinae and Ponerinae, as Emery has contended, and that we might unite them with either. I should prefer, however, to separate them out as an independent subfamily, which may be ascribed to Forel, who in 1893 first recognized the "Cerapachysii" as a natural tribe. Of course, the name Pro-dorylinae Emery cannot be used for the subfamily, because there is no genus *Prodorylus*.

For many years I have deemed it necessary to introduce another nomenclatorial change, namely that of the subfamily name Camponotinae to Formicinae. Forel, in his study of the poison apparatus and anal glands of ants, published in 1878, divided the subfamily Formicidae Mayr (1855) into two subfamilies, which he called Camponotidae and Dolichoderidae. This was unjustifiable according to our present rules of nomenclature, for Mayr's name should have been retained and restricted to the group containing the genus *Formica*. At that time, which antedated the use of *ina* as a subfamily suffix, Forel justified his course on the ground that "Formicidae" was already in use as a family name.

Owing to the fact that definite rules and conventions in regard to the suffixes of family and especially of subfamily names in Zoölogy have been stabilized only within recent decades, there is considerable confusion concerning the authors to whom our modern names in *ida* and *ina* are to be attributed. It seems to be customary to accredit a family or subfamily name to the author who first recognized the group as supergeneric and gave it a Latin or Greek name based on that of one of its genera. If this is done in the case of the Formicidae the authorities cited in the literature require revision. Frederick Smith (1851), Westwood (1840), Shuckard (1840) and Stephens (1829) all attribute Formicidae as a family name to Leach. They appear to refer to his article published in the Edinburgh Encyclopædia in 1815, where he used the term

Formicarides, or to some later work which I have not seen. Latreille, however, as early as 1810, used Formicarii as a family name, and it would seem to be permissible to cite him as the author of Formicidæ. The subfamily Dorylinæ is attributed by Emery and others to Shuckard (1840), but this author says: "Mr. Haliday has first raised them to a family equivalent to the whole of the social Ants, etc." and at p. 195 he definitively attributes the Dorylidæ to Haliday. This may have been based on correspondence as I find no mention of the term in such published writings of Haliday as I have seen. But the matter is of little moment because Leach, in the 1815 paper referred to above, created a family Dorylida, so that, unless there is an earlier authority, the subfamily Dorylinæ should be accredited to this early British entomologist. Forel attributes the subfamilies Ponerinæ and Myrmicinæ to Lepeletier, but Dalla Torre gives Mayr as the author of the latter and Donisthorpe refers the Ponerinæ also to Mayr. Smith regarded himself as the authority for Poneridæ and Myrmi-

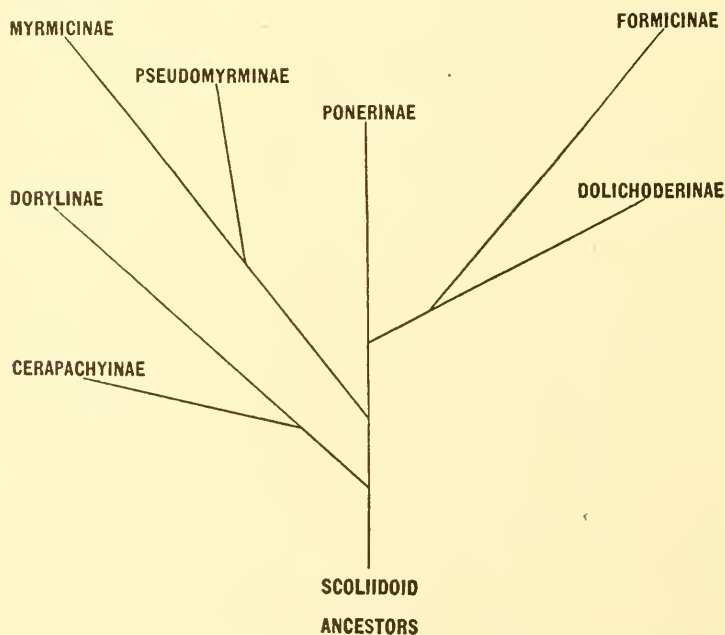


Fig. 3. Phylogenetic relationships of the seven subfamilies of Formicidae.

cidæ. It is clear, nevertheless, that not only the Ponerinæ and Myrmicinæ but also the Formicinæ are to be referred to Lepeletier (1836), who called them respectively the tribes Ponérites, Myrmicites and Formicites, the last, like Mayr's subfamily Formicidæ, being made to include both the modern Dolichoderinæ Forel and Formicinæ (Camponotinæ Forel).

The phylogenetic relations of the seven subfamilies, as understood at the present time, are indicated in the accompanying diagram (Fig. 3). For taxonomic purposes they may be most conveniently arranged in the following linear sequence:

Family Formicidæ Latreille (1910).

- Subfamily 1. Dorylinæ (Leach 1815)
2. Cerapachyinæ (Forel 1893)
 3. Ponerinæ (Lepeletier 1836)
 4. Pseudomyrminæ (Emery 1899)
 5. Myrmicinæ (Lepeletier 1836)
 6. Dolichoderinæ (Forel 1878)
 7. Formicinæ (Lepeletier 1836)

In conclusion I may add that while working on the ants of the Belgian Congo and constructing dichotomic keys for the identification of the genera and subgenera of the world, I have been led to adopt the following new names based on previously described species:

Phrynoponera gen. nov. (Genotype: *Bothroponera gabonensis* Ern. André)

Viticola gen. nov. (Genotype: *Sima tessmanni* Stitz)

Macromischoides gen. nov. (Genotype: *Macromischa aculeata* Mayr)

Hypocryptocerus subgen. nov. (Subgenotype: *Formica hamorrhoidalis* Latreille)

Heteromyrmex gen. nov. (Genotype: *Vollenhovia rufiventris* Forel.)

Diodontolepis gen. nov. (Genotype: *Melophorus spinisquamis* Ern. André)

Pseudaphomomyrmex gen. nov. (Genotype: *Aphomomyrmex emeryi* Ashmead)

Cladomyrma gen. nov. (Genotype: *Aphomomyrmex hewitti* Wheeler).

LITERATURE.

1905. ASHMEAD, W. H. A Skeleton of a New Arrangement of the Families, Subfamilies, Tribes and Genera of the Ants, or the Superfamily Formicoidea. *Canad. Ent.* 1905, pp. 381-384.
1877. EMERY, C. Saggio di un Ordinamento Naturale dei Myrmicidei e Considerazioni sulla Filogenesi delle Formiche. *Bull. Soc. Ent. Ital.* 9, 1877, pp. 67-81, 1 pl.
1895. EMERY, C. Die Gattung *Dorylus* Fabr. und die systematische Eintheilung der Formiciden. *Zoöl. Jahrb. Abt. Syst.* 8, 1895, pp. 685-778, 3 pls., 41 text-figs.
1899. EMERY, C. Intorno alle Larve di Alcune Formiche. *Mem. R. Accad. Sc. Ist. Bologna* 8, 1899, pp. 3-10, 2 pls.
1909. EMERY, C. Beiträge zur Monographie der Formiciden des paläarktischen Faunengebietes. *Deutsch. Ent. Zeitschr. Teil VIII Ponerinæ*, 1909, pp. 355-376.
- 1910-12. EMERY, C. *Dorylinæ* (1910), *Ponerinæ* (1911) and *Dolichoderinæ* (1913) in Wytzman's "Genera Insectorum."
1914. EMERY, C. Intorno alla Classificazione dei "Myrmicinae." *Rend. R. Accad. Sc. Ist. Bologna* 1914, pp. 29-42.
1878. FOREL, A. Der Giftapparat und die Analdrüsen der Ameisen. *Zeitschr. wiss. Zoöl.* 30, 1878, pp. 28-66, 2 pls.
1893. FOREL, A. Sur la Classification de la Famille des Formicides avec Remarques Synonymiques. *Ann. Soc. Ent. Belg.* 37, 1893, pp. 161-167.
1919. GALLARDO, A. Una nueva Prodorilina *Acanthostichus afflictus*. *Anal. Mus. Nac. Hist. Nat. Buenos Aires* 30, 1919, pp. 237-242, 3 figs.
1815. LEACH, W. E. Article "Entomology" in Brewster's *Edinburgh Encyclopædia*, 1815, pp. 57-172.
1836. LEPELETIER, A. DE ST. FARGEAU. *Histoire Naturelle des Insectes. Hyménoptères*, 1, 1836. Paris, de Roret.
1855. MAYR, G. *Formicina Austriaca*. *Verh. zoöl. bot. Ver. Wien* 5, 1855, pp. 373-478, 1 pl.
1877. MAYR, G. Gruppierung der Myrmiciden. *Sitzb. zoöl. bot. Ges. Wien*, 27, 1877, 4 pp.

1840. SHUCKARD, W. E. Monograph of the Dorylidae, a Family of Hymenoptera Heterogyna. Ann. Nat. Hist. 5, 1840, pp. 188-231.
1851. SMITH, F. List of the British Animals in the Collection of the British Museum. 4, Hymenoptera Aculeata. London 1851, 134 pp.
1829. STEPHENS, J. F. A Systematic Catalogue of British Insects. London, Baldwin and Cradock, 1829.
1840. WESTWOOD, J. O. Introduction to the Modern Classification of Insects. Vol. 2, London, 1840.
- 1918a. WHEELER, W. M. The Australian Ants of the Ponerine Tribe Cerapachyini. Proc. Amer. Acad. Arts Sc. 53, 1918, pp. 215-265, 17 figs.
- 1918b. WHEELER, W. M. A study of Some Ant Larvæ, with a Consideration of the Origin and Meaning of the Social Habit among Insects. Proc. Amer. Phil. Soc. 57, 1918, pp. 293-343, 12 figs.
- 1919a. WHEELER, W. M. The Ants of the Genus *Metapone* Forel. Ann. Ent. Soc. Amer. 12, 1919, pp. 173-191, 7 figs.
- 1919b. WHEELER, W. M. A Singular Neotropical Ant (*Pseudomyrma filiformis* Fabricius). Psyche 26, 1919, pp. 124-131, 3 figs.

ODONATA OF CHATHAM, MASSACHUSETTS.

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The following list of Odonata includes material collected last summer at Chatham, and also that taken on various excursions to the surrounding towns. Mr. C. W. Johnson had collected a few species at Eastham of which I make mention, and other species have been recorded from Provincetown, Cotuit, Hyannisport, Woods Hole, Martha's Vineyard, the Elizabeth Islands, beside those listed by the author from Nantucket (May, 1919, report Maria Mitchell Association), and from Wareham (Psyche 26: June, 1919). Specimens of all recorded material are in the author's collection.